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THE BIOLOGY OF DEATH: I—THE PROBLEM[1]

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1. INTRODUCTION

PROBABLY no subject so deeply interests human beings as that of the duration of human life. Presumably just because the business of living was such a wonderfully interesting and important one from the viewpoint of the individual, man has endeavored, in every way he could think of, to prolong it as much as possible. He has had recourse to both natural and supernatural schemes for attaining this objective. On the mundane plane he has developed the sciences and arts of biology, medicine and hygiene, with the fundamental purpose of stretching the length of each individual's life on earth to the greatest attainable degree. Recognizing pragmatically, however, that at best the limitations in this direction were distinctly narrow, when conceived in any historical sense, he has with singularly wide-spread unanimity, deemed it wise to lay a hedging bet upon a horse of another color. Man's body plainly and palpably returns to dust, after the briefest of intervals, measured in terms of cosmic evolution. But there is nothing in this fact which precludes the postulation of an infinite continuation of that impalpable portion of man's being which is called the soul. With the field thus open we see some sort of notion of immortality incorporated in an integral part of almost all folk philosophies of which any record exists.

Now, perhaps unfortunately, perhaps fortunately, it has up to the present time proved impossible absolutely to demonstrate, for reasons which will presently appear, by any scientifically valid method of experimentation or reasoning, that any real portion of that totality of being which is an individual living man persists after he dies. Equally, for the same reasons, science can not absolutely demonstrate that such persistence does not occur. The latter fact has had two important consequences. In the first place, it has permitted many millions of people to derive a real comfort of soul in sorrow, and a fairly abiding tranquility of mind in general from the *belief* that immortality is a reality. Even the most cynical of scoffers can find little fault with such a result, the world and human nature being constituted as they are. The other consequence of science's present inability to lay bare, in final and irrefragable terms, the truth about the course, if any, of events subsequent to death is more serious. It opens the way for recurring mental epidemics of that intimate mixture of hyper-credulity, hyper-knavery, and unsatisfied Freudian urges, which used to be called spiritualism, but now usually prefers more seductive titles. We are at the moment in the midst of perhaps the most violent and destructive epidemic of this sort which has ever occurred. Its evil lies in the fact that in exact proportion to its virulence it destroys the confidence of the collective mind of humanity in the enduring efficacy of the only thing which the history of mankind has demonstrated to contribute to the real advancement of his intellectual, physical, spiritual and moral well being, namely that orderly progression of ascertained knowledge which we now call *science.*

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[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University, No. 28.

This, and the papers which will follow it under the same general title are based upon a series of lectures recently given at the Lowell Institute in Boston.

The reason why science finds itself helpless to prevent spiritualism's insidious sapping of the intellectual fiber of the race is because it is asked to prove a negative, upon the basis of unreal data. How difficult such a task is is obvious as it is proverbial. Until science has demonstrated that there is *not* a continuation of individual supernatural existence after natural death, the spiritualist can, and will, come forward with supposed demonstrations that there is such a continuation. But the most characteristic feature of science is its actuality, its reality, its naturality. Pearson has pointed out, in characteristically clear and vigorous language, the reason why, in the minds of uninformed persons, science appears helpless in this situation. He says:

> Scientific ignorance may either arise from an insufficient classification of facts, or be due to the unreality of the facts with which science has been called upon to deal. Let us take, for example, fields of thought which were very prominent in medieval times, such as alchemy, astrology, witchcraft. In the fifteenth century nobody doubted the "facts" of astrology and witchcraft. Men were ignorant as to how the stars exerted their influence for good or ill; they did not know the exact mechanical process by which all the milk in a village was turned blue by a witch. But for them it was nevertheless a fact that the stars did influence human lives, and a fact that the witch had the power of turning the milk blue. Have we solved the problems of astrology and witchcraft today?
>
> Do we now know how the stars influence human lives, or how witches turn milk blue? Not in the least. We have learnt to look upon the facts themselves as unreal, as vain imaginings of the untrained human mind; we have learnt that they could not be described scientifically because they involved notions which were in themselves contradictory and absurd. With alchemy the case was somewhat different. Here a false classification of real facts was combined with inconsistent sequences—that is, sequences not deduced by a rational method. So soon as science entered the field of alchemy with a true classification and a true method, alchemy was converted into

chemistry and became an important branch of human knowledge. Now it will, I think, be found that the fields of inquiry, where science has not yet penetrated and where the scientist still confesses ignorance, are very like alchemy, astrology, and witchcraft of the Middle Ages. Either they involve facts which are in themselves unreal—conceptions which are self-contradictory and absurd, and therefore incapable of analysis by the scientific or any other method—or, on the other hand, our ignorance arises from an inadequate classification and a neglect of scientific method.

This is the actual state of the case with those mental and spiritual phenomena which are said to lie outside the proper scope of science, or which appear to be disregarded by scientific men. No better example can be taken than the range of phenomena which are entitled Spiritualism. Here science is asked to analyse a series of facts which are to a great extent unreal, which arise from the vain imaginings of untrained minds and from atavistic tendencies to superstition. So far as the facts are of this character, no account can be given of them, because, like the witch's supernatural capacity, their unreality will be found at bottom to make them self-contradictory. Combined, however, with the unreal series of facts are probably others, connected with hypnotic and other conditions, which are real and only incomprehensible because there is as yet scarcely any intelligent classification or true application of scientific method. The former class of facts will, like astrology, never be reduced to law, but will one day be recognized as absurd; the other, like alchemy, may grow step by step into an important branch of science. Whenever, therefore, we are tempted to desert the scientific method of seeking truth, whenever the silence of science suggests that some other gateway must be sought to knowledge, let us inquire first whether the elements of the problem, of whose solution we are ignorant, may not after all, like the facts of witchcraft, arise from a superstition, and be self-contradictory and incomprehensible because they are unreal.

Let us recapitulate briefly our discussion to this point. Mankind has endeavored to prolong the individual life by natural and by supernatural means. This latter plan falls outside the present purview of the scientific method. The former is, in last analysis, responsible for the development of the science of biology, pure and applied, and the arts which found their operations upon it. Biology can and has contributed much to our knowledge of natural death and the causes which determine the duration of life. It is the purpose of this series of lectures to review this phase of biological science, and endeavor to set forth in an orderly and consistent manner the present state of knowledge of the subject.

2. The Problem

The problem of natural death has two aspects, one general, the other special. These may be stated in this way:

1. Why do living things die? What is the meaning of death in the general philosophy of biology?
2. Why do living things die *when* they do? What factors determine the duration of life in general and in particular, and what is the relative influence of each of these factors in producing the observed result?

Both of these problems have been the subject of much speculation and discussion. There has accumulated, especially in recent years, a considerable amount of new experimental and statistical data bearing upon them. I hope to be able in what follows to show that this new material, together with that which has for a long time been a part of the common store of biological knowledge, makes possible a clearer and more logically consistent picture than we have had of the meaning of death and the determination of longevity. Let us first examine in brief review the broad generalizations about death which have grown up in the course of the development of biology, and which may now be regarded as agreed to by practically all biologists.

3. Biological Generalizations About Natural Death

The significant general facts which are known about natural death are these:

(a). *There is an enormous variation in the duration of life, both intra and inter-racially.* Table 1, which is adapted from various authorities, is to be read with the understanding that the figures are estimates frequently based upon somewhat general and inexact evidence, and record extreme, though it is believed authentic instances. While the figures, on the accounts which have been mentioned, are subject to large probable errors, the table does give a sufficiently reliable general picture of the truth to indicate the enormous differences which exist among different forms of animal life in respect of longevity.

TABLE 1
Longevity of Animals

Animal	Approximate limits of maximum duration of life in different species
Lower invertebrates	24 hours to?
Insects	24 hours to 17 years
Fish	? to 267 years
Amphibia	? to 36 years
Reptiles	? to 175 years
Birds	9 years to 118 years
Mammals	1½ years to over 100 years

We see from this table that life may endure in different forms from only the briefest period, measured in hours as in the case of *Ephemeridae,* to somewhere in the hundreds of years. The extremely long durations are of course to be looked upon with caution and reservation, but if we accept only extreme cases of known duration of life in man, the range of variation in this characteristic of living things is sufficiently wide.

It is probable that man, in exceptional instances, is nearly the longest lived of all mammals. The common idea that whales and elephants attain great longevity appears not to be well founded. The absolutely authentic instances of human survival beyond a century are, contrary to the prevalent view and customary statistics, extremely rare. The most painstaking and accurate investigation of the frequency of occurrence of centenarians which has ever been made is that of T. E.

Young. Because of the considerable intrinsic interest of the matter, and the popular misconceptions which generally prevail about it, it will be worth while to take a little time to examine Young's methods and results. He points out in the beginning that the evidence of great age which is usually accepted by census officials, by registrars of death, by newspaper reporters, and by the general public, is, generally speaking, of no validity or trustworthiness whatever. Statements of the person concerned, or of that person's relatives or friends, as to extreme longevity, can almost invariably be shown by even a little investigation to be extremely unreliable. To be acceptable as scientific evidence, any statement of great age must be supported by unimpeachable *documentary* proof of at least the following points:

a. The date of *birth,* or of baptism.
b. The date of *death.*
c. The *identity* of the person dying at a supposed very advanced age with the person for whom the birth or baptismal record, upon which the claim of great age is based, was made out.
d. In the case particularly of married women the date of *marriage,* the person to whom married, and any other data which will help to establish proof of identity.

In presumptive cases of great longevity, which on other grounds are worthy of serious consideration, it is usually in respect of item c—the proof of identity—that the evidence is weakest. Every student of genealogical data knows how easy it is for the following sort of thing to happen. John Smith was born in the latter half of the eighteenth century. His baptism was duly and properly registered. He unfortunately died at the age of say 15. By an oversight his death was not registered. In the same year that he died another male child was born to the same parents, and given the name John Smith, in commemoration perhaps of his deceased brother. This second John Smith was never baptized. He attained the age of 85 years, and then because of the appearance of extreme senility which he presented, his stated age increased by leaps and bounds. A study of the baptismal records of the town disclosed the apparent fact that he was just 100 years old. The case goes out to the public as an unusually well authenticated case of centenarianism, when of course it is nothing of the sort.

Young applies rigidly the criteria above enumerated first, to the historically recorded cases of great longevity such as Thomas Parr, *et id genus omne,* and rejects them all; and second to the total mortality experience of all the Life Assurance and Annuity Societies of Great Britain and the annuity experience of the National Debt Office. The number of persons included in the experience was close upon a million. He found in this material, and from other outside evidence, exactly 30 persons who lived 100 or more years. In Table 2 the detailed results of his inquiry are shown in condensed form.

TABLE 2

Authentic Instances of Centenarianism (from Young)

Sex	Social status (single or married)	Age at death (or living)		
		Years	Months	Days
♀	M	110	..	321
♀	M	108	..	144
♀	M	105	8	...
♀	S	104	9	16
♀	M	103	9	28
♀	?	103	..	269
♀	M	103	3	7
♂	?	103	1	8
♂	?	102	9	2
♀	?	102	..	218
♀	S	102	2	10
♀	S	102	1	8
♀	S	102	..	21
♀ *	S	102	..	19
♂	?	102	..	2
♀ **	S	101	10	4
♀	S	101	8	25
♂	?	101	..	263
♂	?	101	4	...
♀	S	101	1	16
♀	S	101	1	4
♂	?	101	..	32
♀	S	101	..	1
♂	?	100	9	4
♀	S	100	7	6
♀	S	100	6	9
♀	M	100	..	133
♂	M	100	2	24
♀	S	100	1	10
♂	?	100	..	20

*Living 30 September, 1905

**Living 31 July, 1898.

It will be noted from this table that the most extreme case of longevity which Young was able to authenticate was about a month and a half short of 111 years. Of the 30 centenarians recorded 21 were women and 9 were men. The superiority of women in expectation of life is strikingly apparent at the very high age of 100 years. We shall later see that this is merely a particularly noteworthy instance of a phenomenon which is common to a great portion of the life span.

The contrast between these proved findings of Young exceedingly modest both in respect of numbers and extremity of longevity, and the loose data on centenarianism which one can find in any year's mortarity statistics, is striking. In an examination of the matter recently I found that in the Registration area of the United States there were recorded in the year 1916, out of a total of 1,001,921 deaths at all ages the following as of ages 100 or over.

White males	137
Colored males	116
White females	180
Colored females	216
Total	649

In this large total 4 persons were recorded as having died at age 120, and one, a colored female, at the preposterous age of 134!

B. *There is no generally valid, orderly relationship between the average duration of life of the individuals composing a species and any other broad fact now known in their life history, or their structure, or their physiology.* Many attempts have been made to set up generalizations establishing connections of this sort. Weismann particularly has endeavored to establish such relations only to have them overthrown sometimes by facts which he himself presents. It has, for example, been contended that the larger an animal the longer its life. This is obviously no general law. Again it has been held that no animal lives after reproducing, except such as care for their young, but almost numberless instances can be adduced where no such relationship holds. It will not pay us to examine all the hypotheses of this general type which have, at one time or another, been put forward. With one exception, to which we shall advert immediately, they all suffer from too many important exceptions to be considered valid generalizations.

C. *Natural death as distinguished from accidental death is preceded by definite structural and functional changes in the body.* These changes in the structure of different organs and parts of the body, and in their manner of functioning constitute the material basis of what is called *senescence* or growing old. Some of the morphological and physiological changes which characterize extreme senescence are apparent and known to all. Such are in case of man the bent posture which means a bending and fusion of the elements of the vertebral column, the wrinkled visage, which denotes a profound alteration of tissue elements, and the shuffling and uncertain gait, which bespeaks a failing motor coordination. In Figure 1 these senescent changes are all well indicated in the case of an old man who has received much newspaper notice during the past year, "Uncle" John Snell of Kentucky, who is here shown with his last wife and supposed son. This poor old man has been exhibited about that part of the country as "The oldest living human being," at a claimed age of 131 years. As a matter of fact, Nascher, who has made a careful investigation of the case, finds him to be "about one hundred years old, possibly a year younger or older." The paternity of the 4½ year old boy, though claimed by Shell, is in considerable doubt.

Besides these obvious senescent changes there are going on even more significent changes in the cellular elements which compose the body. Certain of these cellular changes of age were fully described, in a brilliant series of Lowell lectures given a little more than a decade ago by a great master of morphological research, the late Dr. Charles Sedgwick Minot. Over a quarter of a century ago Hodge made a careful study of senile changes in nerve cells. In a man dying naturally at 92 years of age he found marked changes in the cells of the spinal ganglia as compared with those of a new born babe. The chief differences are exhibited in Table 3.

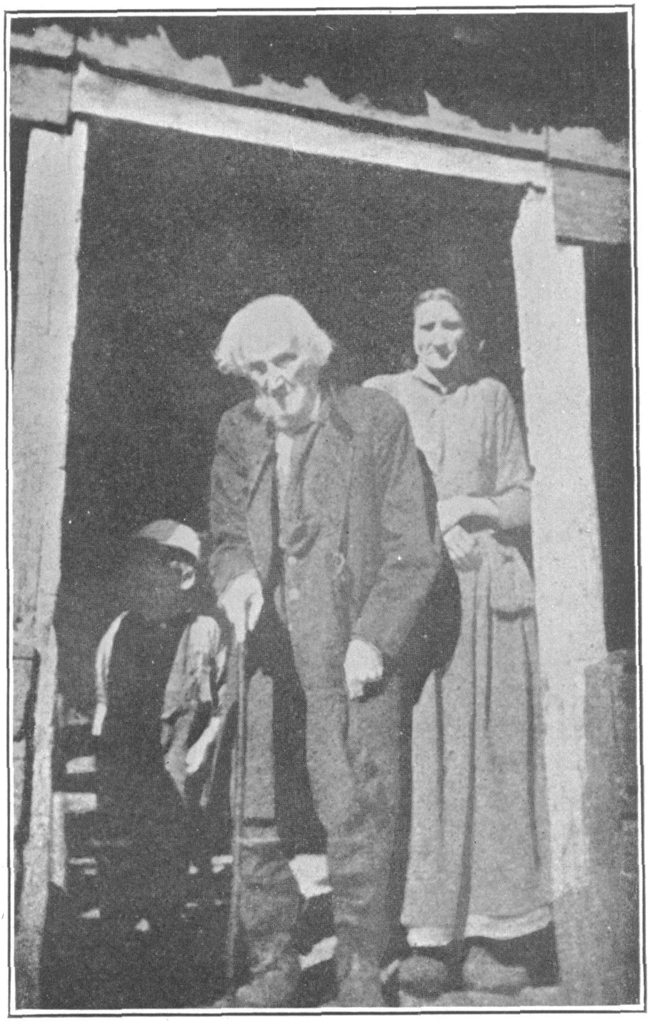

FIG. 1. PHOTOGRAPH OF JOHN SHELL, CLAIMED TO BE 131 YEARS OLD, BUT ACTUALLY ABOUT 100, WITH HIS WIFE AND PUTATIVE SON. (From Nascher).

TABLE 3

Showing the Principal Differences Observed on Comparing the Spinal Ganglion Cells (First Cervical Ganglion) from a Child at Birth With Those from a Man Dying of Old Age at Ninety-two Years.
(From Hodge's data)

	Baby at birth. Male	Old Man
Volume of nucleus	100 per cent.	64.2 per cent.
Nucleoli visible	53 per cent.	5 per cent.
Deep pigmentation	0 per cent.	67 per cent.
Slight pigmentation	0 per cent.	33 per cent.

Hodge found still more marked changes in the antennary lobe of the nervous system of the honey bee. The nature of the changes is shown in Figure 2.

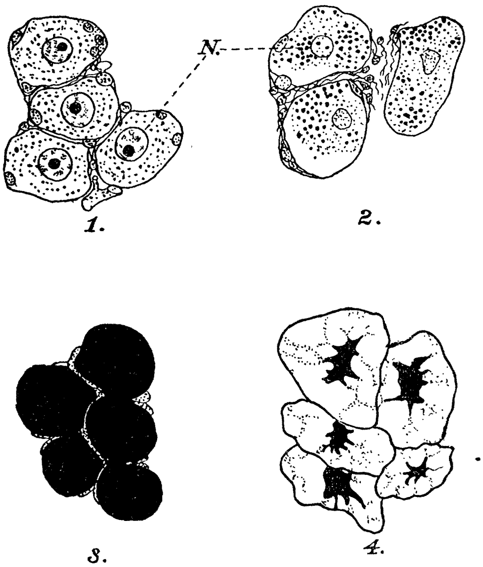

FIG 2. SHOWING THE CHANGES IN NERVE CELLS DUE TO AGE. 1, spinal ganglion cells of a still-born male child; 2, spinal ganglion cells of a man dying at ninety-two years; N. nuclei. In the old man the cells are not large, the cytoplasm is pigmented, the nucleus is small, and the nucleolus much shrunken or absent. Both sections taken from the first cervical ganglion, X 250 diameters; 3, nerve cells from the antennary ganglion of a honey-bee. just emerged in the perfect form; 4, cells from the same locality of an aged honey-bee. In 3, the large nucleus (black) is surrounded by a thin layer of cytoplasm. In 4, the nucleus is stellate, and the cell substance contains large vacuoles with shreds of cytoplasm. (From Donaldson after Hodge).

In the ganglion cells of both man and the honey bee, the volume of the nucleus in proportion to that of the rest of the cell body becomes reduced with advancing age. Dr. Minot showed that this was a very general phenomenon in senescence, and was a continuous process from birth to death. He gave to it and related and associated cellular changes the name "cytomorphosis," and attributed to it the greatest significance in bringing about senescence and death. As we shall presently see, cytomorphosis may perhaps more justly be regarded as one of the morphological results of senescence rather than its cause.

Recently Mrs. Pixell-Goodrich, an English worker, has re-studied the senescent changes in the cells of the honey bee. Her work shows in a striking way the loss of protoplasm in the aged cell. In the young bee immediately after hatching, the cells are large and plump, only separated from each other by narrow strands of connective tissue. In the same region of the same ganglion in an old bee which came from a hive on a fine day in March, but was too weak to effect a cleansing flight and soon became moribund, the nerve cells were quite worn out. There was left only a framework of connecting tissue, with an occasional nucleus of a nerve cell in a more or less necrotic condition, with only a little cytoplasm around it.

There are other, and perhaps even more general and striking morphological changes in senescence than the changed relation between cytoplasm and nucleus. Conklin says:

> By all odds the most important structural peculiarity of senescence is the increase of metaplasm or differentiation products at the expense of the general protoplasm. This change of general protoplasm into products of differentiation and of metabolism is an essential feature of embryonic differentiation and it continues in many types of cells until the entire cell is almost filled with such products. Since nuclei depend upon the general protoplasm for their growth, they also become small in such cells. If this process of the transformation of protoplasm into differentiation products continues long enough it necessarily leads to the death of the cell, since the continued life of the cell depends upon the interaction between the general protoplasm and the nucleus. In cells laden with the products of differentiation, the power of regulation is first lost, then the power of division, and finally the power of assimilation; and this is normally followed by the senescence and death of the cells.

D. *Natural death (as distinguished from accidents) occurs normally and necessarily only in animals composed of many cells.* Unicellular organisms are finally known, chiefly as the result of the brilliant and painstaking researches of Woodruff and his students, to be immortal *in esse* as well as *in posse*. Since the discovery by Woodruff and Erdmann of the process of nuclear reorganization, which they call endomixis, this conclusion is as solidly grounded if we regard a cycle of protozoan divisions as the homologue of the metazoan body, as it is if we consider each individual protozoan as such homologue. Woodruff has been cultivating the common unicellular form *Paramecium*, shown in Figure 3, for over 13 years.

During all this time no conjugation or pairing of individuals has occurred. In a recent letter Dr. Woodruff says: "After we had discovered and worked out endomixis there seemed no particular use of carefully recording the number of generations each day. But the culture is still going on as well as ever and is at approximately the 8500th generation—13½ years old! On May 1st, 1915, (just 8 years old) it was at the 5071st generation." If in 8,500 generations—a duration of healthy reproductive existence which, if the generation were of the same length as in man would represent roughly a quarter of a million years in absolute time,—natural death has not occurred, we may with reasonable assurance conclude that this animal is immortal.

The distinction between Protozoa and Metazoa in respect of the incidence of natural death is so important that it requires a somewhat detailed explanation, together with the reasons for it. Protozoa reproduce by a process of simple division or fission. A particular individual after growing to a certain size simply divides transversely into two like individuals, at first smaller in size, but rapidly growing to full adult magnitude. The essential gross features of this process are illustrated in Figure 4. One can not say which is parent and which is offspring. One individual simply becomes two. Upon occasion another process known as *conjugation* may intervene.

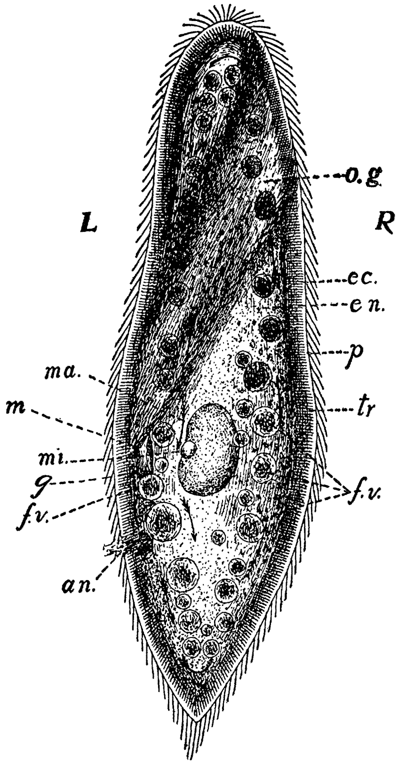

FIG. 3. PARAMECIUM, VIEWED FROM THE ORAL SURFACE. *L*, left side; *R*, right side; *an.*, anus; *ec.*, ectosarc; *en.*, endosarc; *f. v.*, food vacuoles; *g*, gullet; *m*, mouth; *ma.*, macronucleus; *mi.*, micronucleus; *o. g.*, oral groove; *P.*, pellicle; *tr.*, trichocyst layer. The arrows show the direction of movement of the food vacuoles. (From Jennings).

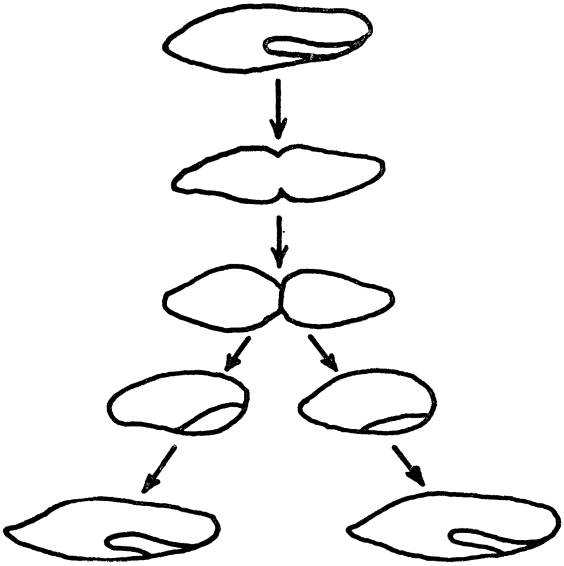

FIG. 4. DIAGRAM SHOWING THE PROCESS OF REPRODUCTION BY FISSION IN THE UNICELLULAR ORGANISM *Paramecium*.

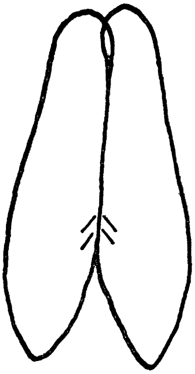

FIG. 5. CONJUGATION IN PARAMECIUM

In this process two individuals mate together. By a process of assortative mating like sizes pair together, as was first shown by the writer and later confirmed by Jennings. After pairing has occurred an interchange of nuclear substance occurs by a complicated mechanism described and figured in many elementary textbooks of zoology. This process of conjugation need not further concern us here, for the reason that Woodruff in the work already referred to has shown that this phenomenon is not essential to the continued life of the race. Its place may be, and normally very frequently is, taken by the process called

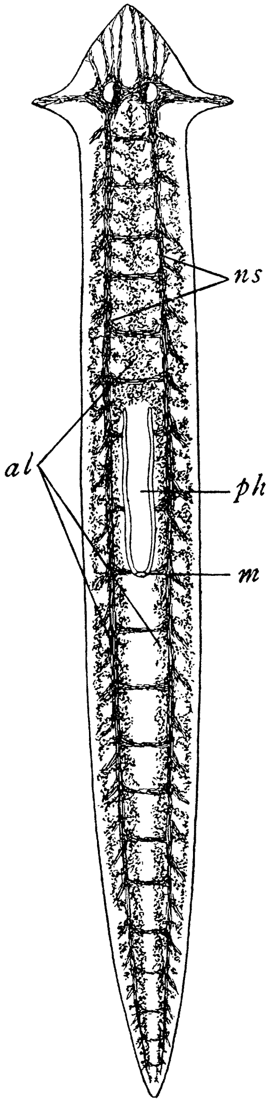

FIG. 6. PLANARIA DOROTOCEPHALA: *m*, mouth; *ph*, pharynx; *al*, alimentary tract; *ns*, nervous system. (From Child).

endomixis. In this process there occurs a nuclear breakdown and reorganization which appears to be the equivalent, functionally at least, of that which takes place during conjugation.

Now it is apparent that there is no place for death in a scheme of reproduction by simple fission such as is illustrated in Figure 4. Nothing is left at any stage to fulfill the proverbial scheme of "dust to dust and ashes to ashes." When an individual is through its single individual existence it simply becomes two individuals, who go merrily on playing the fascinating game of living here and now. There is, in short, no hope that messages will be received from Paramecia in the spirit world, for the simple reason that there is no chance for the soul of a Paramecium—assuming for the argument that he has one—to get there.

In a few of the simplest and most lowly organized groups of many-celled animals or Metazoa this power of multiplication by simple fission, or budding off a portion of the body which reproduces the whole, is retained as a facultative asset. This process of reproduction in which the somatic or body cells of one generation produce the

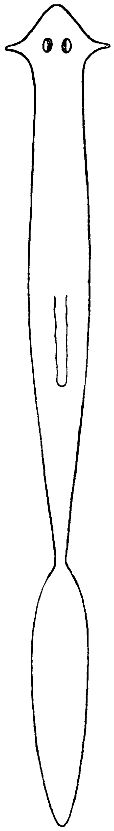

FIG. 7. BEGINNING OF PROCESS OF AGAMIC REPRODUCTION BY FISSION IN PLANARIA (From Child).

somatic cells of the next generation has been called agamic reproduction. It occurs as the more usual but not exclusive mode of reproduction, in some or all forms of the three lowest groups of multicellular organisms, the sponges, flatworms, and coelenterates. More rarely it may occur in other of the lower invertebrate groups. It may occur in the form of budding or of fission comparable to that of the *Protozoa*. The agamic reproduction of one of the flatworms, *Planaria dorotocephala*, studied by the writer many years ago, shown in Figure 6, may serve as an illustration.

This simply organized worm, which lives under stones in sluggish streams and ponds, after attaining a certain size, will under the appropriate environmental conditions exhibit a constriction towards the posterior end of the body, as shown in Figure 7.

For a time the animal moves about as a rather ungainly double individual. It finally separates into two. The larger anterior part forms a new tail, and the smaller posterior fission product forms a new head and rapidly grows to full size. The process is in principle exactly the same as the multiplication of Paramecium by fission. In another member of the same general group of animals as *Planaria*, named *Stenostomum*, several fission planes may form and the process start anew before the products delimited by the first plane have separated. As a result we get frequently in this form chains of individuals attached in a long string to each other, as shown in Figure 8.

It is obvious that so long as reproduction goes on in this manner in these multicellular forms there is no place for death. In the passage from one generation to the next no residue is left behind. Agamic reproduction, and its associated absence of death occurs very commonly in plants. Budding and propagation by cuttings are the common forms in which it is seen. The somatic cells have the capacity of continuing multiplication and life for an indefinite duration of time, so long as they are not accidentally caught in the breakdown and death of the whole individual in which they are at the moment located. Thus virtually every apple tree in every orchard in this country is simply a developed branch or bud of some original apple tree from which it was cut, in many cases centuries ago. Apple trees can not of their own unaided efforts propagate either buds or cuttings. So until the intervention of man apple trees died natural deaths, somatically speaking, just as do the higher animals of which we shall speak presently. But their cells were inherently capable of better things, as was demonstrated when man first cut off a shoot from an old apple tree and provided it with a root by grafting.[2] Then it went on and made a new tree. From it in turn cuttings were taken, and so the process has continued to the present day. A part of the soma of one generation produces the soma of the next generation and goes on living indefinitely.

A different mode of reproduction is characteristic of higher multicellular animals, and in all but the lowest groups is the exclusive method. A new individual is started by the union of two peculiar cells of extraordinary potentialities, called germ cells. These germ cells are of two sorts, ova and spermatozoa. In bisexual organisms the former are borne in the female, and the latter in the male body. Both sorts undergo a complicated preparation for union, the result of which is that when union does occur each party to it contributes either an exactly equal or an approximately equal amount of hereditary material. After union has taken place the fertilized ovum or zygote

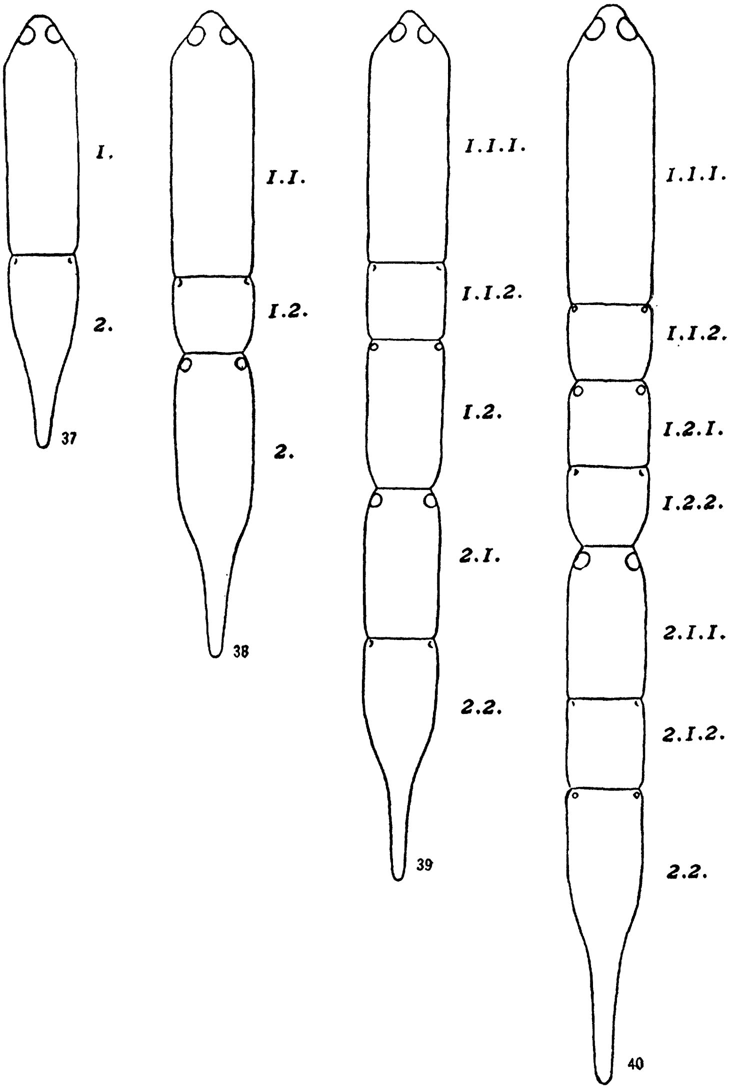

FIG. 8. PROGRESS OF AGAMIC REPRODUCTION IN STENOSTOMUM: the sequence in the formation of new zooids is indicated by the numerals. (From Child).

presently begins to divide, first into two cells, these again to four, and so on until by a continuation of this process of division with concomitant differentiation the whole body is formed. As the animal develops by repeated cell division and differentiation it is frequently found that at a very early stage the cells which are to be the germ cells of the next generation are clearly recognizable by their structure, and often are set aside in a definite location in the developing embryo. Thus, to take out a single example of phenomenon of wide generality, at a very early stage in the development of the dog-fish, when the only bodily organs of which even the rudiments are recognizable are the beginnings of what will presently become the spinal cord and the backbone, it was shown by Woods many years ago that the germ cells are definitely localized and recognizable, as shown in Figure 9.

In some forms, notably the round-worm *Ascaris,* various crustacea and insects, the cells which are to become germ cells are visibly set apart from the very first or one of the first three or four cleavages of the fertilized ovum. For example, in the case of the crustacean *Cyclops* Amma has shown that the granules visible at one pole in the very first division mark the prospective germ path, as shown in Figure 10.

In the gnat *Chironomus* the same thing is visible at a very early cleavage, according to the observations of Harper. For the most comprehensive and critical review in existence of the extensive literature on the *Keimbahn* one should consult the recent contributions of Hegner on the subject.

To condense a long and complicated matter we may state the situation regarding reproduction and death in the *Metazoa* in this way. A higher, multicellular individual may be conceived, from the viewpoint of the present discussion, as composed of two essentially independent portions, the germ cells on the one hand, which are immortal in the same sense that the Protozoa are immortal, and the rest of the body, which it is convenient to call technically the soma, on the other hand. The soma undergoes natural death after an interval of time which as we have seen varies from species to species. The germ cells which the individual bears in its body at the time of its death of course die also. But this is purely accidental death so far as concerns the germ cells. Such of them as were, prior to the death of the soma, enabled to unite with other germ cells went on living just as does the dividing *Paramecium.* Reduced to a formula we may say that the fertilized ovum (united germ cells) produces a soma, and more germ cells. The soma eventually dies. Some of the germ cells, prior to that event produce somata and more germ cells, which in turn produce somata and germ cells, and so on in a continuous cycle which has never yet ended since the appearance of multicellular organisms on the earth.

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[2] This provision of roots was not essential, only practically convenient. The cutting would, if enough pains were taken, grow its own roots.

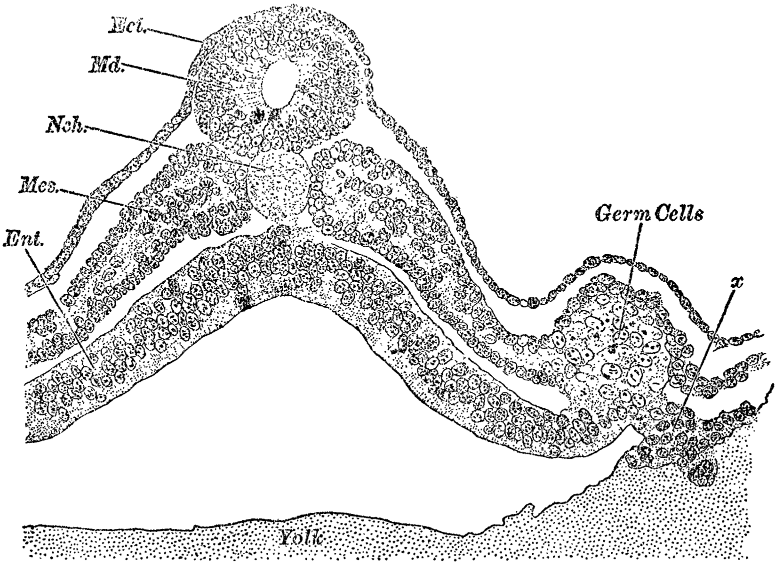

FIG. 9. SECTION ACROSS THE POSTERIOR PART OF AN EMBRYO DOG-FISH (ACANTHIAS) OF 3.5 MM., to show the compact cluster of germ cells on one side. The germ cells in later stages migrate from this primitive position, moving singly or in small groups. *Ect,* ectoderm; *Md,* medullary canal or primitive spinal cord; *Nch,* notochord; *Mes,* mesoderm; *Ent,* entoderm; *X,* cellular strand connecting the germ cell cluster with the yolk. (From Minot after Woods, with permission of the publishers, G. P. Putnam's Sons).

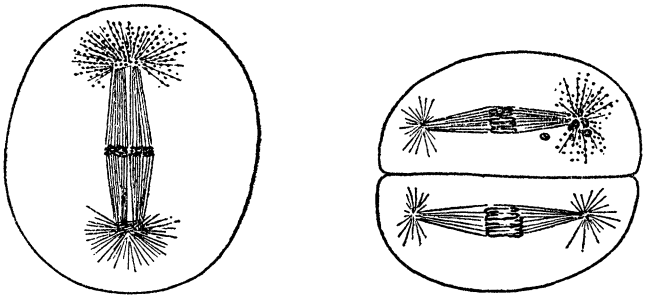

FIG. 10. FIRST AND SECOND DIVISION IN EGG OF CYCLOPS, showing at one pole of spindle the granules which mark the germ path. (From Child, after Amma, by permission of University of Chicago Press).

The contrast between the protozoan and the metazoan method of descent is shown in Figure 11, which is a modification of a similar diagram originally due to my colleague, Dr. H. S. Jennings.

The diagram represents the descent of generations. The upper portion of the diagram shows the mode of descent in forms reproducing from organisms reproducing from a single parent. The lower, or B portion of the diagram shows the mode of descent in form reproducing from two parents. The lines represent the lives of individuals (as in A diagram) or of germ cells (in the B diagram) beginning at the left and passing to the right. In the A diagram which represents uniparental reproduction by fission the line of ancestry traced back from any individual at the right is always single, and there is no corpse to be found anywhere, each present body transforming directly into the two bodies of the next generation. In the B diagram where we have biparental reproduction by the union of germ cells, as in man, the solid black triangles represent the bodies, or somata, and the lines the germ cells. A line of ancestry traced back from any individual towards the right end of the diagram forks at each generation, and in comparatively few generations one has a multitude of ancestors. The *bodies* of one generation have no continuity with the bodies of the previous or the following generation. In each generation the soma dies while new somata are produced by the union of germ cells from diverse lines.

E. *Life itself is a continuum.* A break or discontinuity in its progression has never occurred since its first appearance. Discontinuity of existence appertains not to life, but only to one part of the makeup of a portion of one large class of living things. This is certain, from the facts already presented. Natural death is a new thing which has appeared in the course of evolution, and its appearance is concomitant with, and evidently in a broad sense, caused by that relatively early evolutionary specialization which set apart and differentiated certain

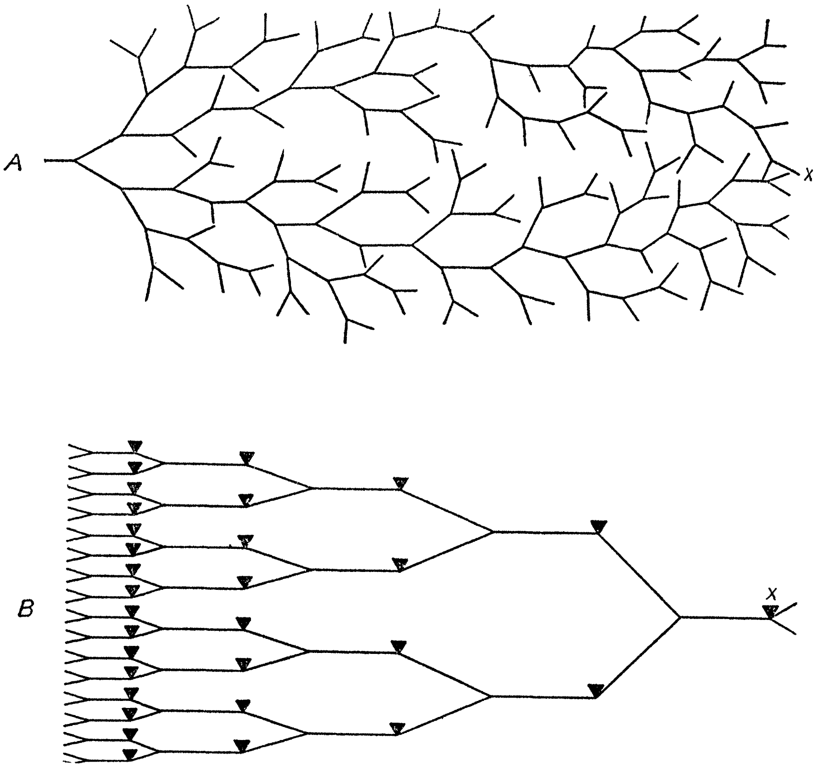

FIG. 11. DIAGRAM TO SHOW MODE OF DESCENT in (A) unicellular animals reproducing agamically, and in (B) multicellular animals reproducing by germ cells. For further explanation see text. (Modified from Jennings).

cells of the organism for the exclusive business of carrying on all functions of the body other than reproduction. We are able to free ourselves, once and for all, of the notion that death is a necessary attribute or inevitable consequence of life. It is nothing of the sort. Life can and does all the time go on without death. The somatic death of higher multicellular organisms is simply the price we pay for the privilege of enjoying those higher differentiations of structure and function which have been added on as a side line to the main business of living things, which is to pass on in unbroken continuity the never-dimmed fire of life itself.

4. THEORIES OF DEATH

On the basis of these five general classes of facts which have been briefly reviewed a whole series of speculations as to the meaning of death have been reared. Of course, theologians have not failed to assay the ore of so valuable a lode. The one interesting thing to note in passing is that the traditional view which the Christian religion takes of death, is in one important respect in complete accord with the results of modern biology. I refer to the recognition that death is not a *necessary* adjunct or "grand characteristic of life itself." In the view of the Church death is a consequence of sin, and prior to the advent of sin living things were in order to continue indefinitely in the enjoyment of life. Now in this statement what the theologian calls sin the biologist calls differentiation. A wonderful sermon could be preached on this identity of sin and differentiation. It has, of course, always been recognized that the sinful was different. Consideration of the matter convinces one immediately that all too frequently in man's sad history here below the different has been regarded as sinful. But as the object of this discussion is not theological I refrain from pursuing further so alluring a theme.

The first attempt at a biological evaluation[3] of the meaning of death which attracted the serious attention of scientific men was that of Weismann. In his famous address of 1881 on the duration of life, Weismann propounded the thesis that death was an adaptation, advantageous to the race, and had arisen and was preserved by natural selection. Probably no more ridicuously absurd and perverse extension of the theory of natural selection than this was ever made. It appeared, however, just at the time when the post-Darwinian attempt to settle the problems of evolution by sheer dialectic was at the zenith of its popularity. Now-a-day such a doctrine as Weismann's would not receive so respectful a hearing.

Metchnikoff, whose views excited so much popular interest some years ago, held that death was the result of intoxication, arising from the absorption of putrefactive products of the activity of intestinal bacteria. For obvious reasons such a view has no general validity and does not touch the philosophical problem of the biological meaning of death. More philosophic developments of the same basic idea have been presented by Jickeli and Montgomery. Both held that because of the mechanical incompleteness of the processes of cellular metabolism injurious and toxic substances tend to accumulate in the cells of the body and that senescence and death are the results of such accumulations.

A much broader, and in the light of all the facts sounder view, is that the determination of degrees of longevity and of the fact of death itself, is inherent in the biological constitution of the individual and the species. This view was expressed by Johannes Müller a quarter of a century ago in his *Physiologie*, by Cohnheim forty years later, and has had many later adherents. I shall return to a discussion of it later.

There have been a number of theories of senescence and death, differing widely in details, but having the one point in common of attributing these phenomena to orderly changes with advancing age in the relative proportion of nucleus to cytoplasm in the cells of the body. Here may be mentioned, without pausing to go into detailed consideration of their different views Verworn, Mühlmann, Richard Hertwig, and Minot.

Another group of hypotheses, all advanced in comparatively recent times and associated with the names of Kassowitz, Conklin, and Child, are developed about the metabolic aspects of age changes. There is observed a decrease in assimilatory capacities of cells with differentiation and age. These metabolic changes are regarded as fundamentally causal of the phenomena of senescence and death. In this general group of hypotheses would belong the views of my colleague, Dr. W. T. Howard.

Benedict in a detailed investigation of senility in plants reaches the conclusion

> "that the duration of life is directly linked with the degree of permeability in that part of the living cell which places it in contact with the universe about it, and that as the activities of life proceed the cell is being gradually entombed by an inevitable decrease in the permeability of its protoplasm.
>
> While decreasing permeability furnishes a possible explanation of the more obvious symptoms of senility, it cannot be the only degeneration of first rank. All protoplasmic functions must be involved. Underlying these primary causes of senile degeneration there must be some general fundamental cause from which they spring. This fundamental cause may well be the colloidal nature of protoplasm."

Delage and Jennings have considered that death is the result of differentiation. Unicellular organisms, as we have seen, do not nor-

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[3] The following brief review of the various biological hypotheses which have been advanced as to the meaning of death is largely based upon and follows the excellent discussion of the matter given by Child in his "Senescence and Rejuvenescence."

mally experience natural death. In the higher organisms there has been a progressive setting apart of cells and tissues to perform *particular* vital functions with a consequent loss of the ability to perform *all* vital functions independently. As soon as any one of these cells or tissues begins for any cause whatever to fail to perform its special function properly it upsets the delicate balance of the whole associated community of cells and tissues. Because of the differentiation and specialization of function the parts are mutually dependent upon each other to keep themselves and the whole going. Consequently any disturbance in the balance which is not promptly righted by some regulatory process must eventually end in death. Essentially this view of the matter has been well set forth by Loeb in his most recent paper on the subject. He says: "All this points to the idea that death is not inherent in the individual cell, but is only the fate of more complicated organisms in which different types of cells or tissues are dependent upon each other. In this case it seems to happen that one or certain types of cells produce a substance or substances which gradually become harmful to a vital organ like the respiratory center of the medulla, or that certain tissues consume or destroy substances which are needed for the life of some vital organ. The mischief of death of complex organisms may then be traced to the activity of a black sheep in the society of tissues and organs which constitute a complicated multicellular organism."

At this point I shall not stay to discuss critically each of the hypotheses so summarily reviewed. Instead I shall make bold to state somewhat categorically my own views on the origin and meaning of death and the determination of longevity, and in what follows shall endeavor to set forth in orderly array the evidence which seems to me to support these views. In this process the relations to the conclusions of earlier investigators of what I shall suggest will, I think, sufficiently appear.

Let us consider, then, the following picture of life and death.

1. Life itself is inherently continuous.

2. Living things, whether single-celled or many-celled organisms, are essentially only physico-chemical machines of extraordinary complexity, but regardless of their degree of complexity only amenable to, and activated in accordance with, physical and chemical laws and principles.

3 The discontinuity of death is not a necessary or inherent adjunct or consequence of life, but is a relative new phenomenon, which appeared only when and because differentiation of structure and function appeared in the course of evolution.

4. Death necessarily occurs only in such somata of multicellular organisms as have lost through differentiation the power of reproducing the whole soma from a part of it, or still possessing such power in their cells, have lost the necessary mechanism for separating a part of the soma from the rest for purposes of agamic reproduction.

5. Somatic death results from an organic disharmony of the whole organism, initiated by the failure of some organ or part to continue in its normal harmonious functioning in the entire differentiated and mutually dependent system. This functional breakdown of a part may be caused in a multitude of ways from external or internal sources. It may manifest itself in a great variety of ways both structurally and functionally. Many of these manifestations which have been regarded as causes of senescence, may more truly be considered concomitant attributes of senescence.

6. As a consequence of our second thesis which postulated life to be a mechanism, death, whether of a single somatic cell or of a whole soma, is a result of physico-chemical changes in the cell or organism and these changes are in accordance with ordinary physico-chemical laws and principles

7. The time at which natural death of the soma occurs is determined by the combined action of heredity and environment. For each organism there is a specific longevity determined by its inherited physico-chemical constitution. This specific longevity is capable of modification, within relatively narrow limits, as a result of the impact of environmental forces, the chief mode of action of the environment being in the direction of determining the rate at which the inherited endowment is used up.

For no one of the separate elements of this picture can I claim any particular originality. Most of them would probably be agreed to at once, at least by some biologists. The need is for a synthesizing into a consistent whole of a wide range of data which have accumulated in various fields of biology about death and the duration of life. Such a synthesis will be attempted in what follows. Generally those who have speculated about the biology of death have drawn their evidence from, or at least had their thinking largely colored by the facts in a relatively small part of the whole field. In particular few biologists have any detailed knowledge of the most impressive mass of material, both in respect of quality and quantity, which exists regarding the duration of life of any organism. I refer, of course, to the enormous volume of rather exact data regarding human mortality. Much of this material, to be sure, wants proper analysis, not only mathematical but biological. But that it is a rich material admits of no doubt.